

Phylogenetic and Taxonomic Studies on *Helonias*, *Ypsilandra* and *Heloniopsis*

I. Comparison of Character States (1)

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Several characters of both pistils and stamens were compared in the 10 species of the three genera; *Helonias*, *Ypsilandra* and *Heloniopsis*. Three styles of *Helonias* are often connate shortly at the base, those of *Ypsilandra* are either partially or entirely connate along their lengths, and those of *Heloniopsis* are always entirely connated to form a single columnar structure. *Helonias* and the two other genera differ not only in the number of ovules per loculus of an ovary, but also in seed morphology. Two species of *Heloniopsis* (*H. leucantha* and *H. umbellata*) develop stipitate ovaries, but there is some intraspecific variation regarding the development of the stipe in both species. Capsules of *Ypsilandra tibetica* tend to be substipitate. There is some morphological difference in the anthers between *Helonias* and *Ypsilandra*, but the anthers of the two genera are both unilocular. There is also some extent of confluence between the thecae of *Heloniopsis*, but the confluent part of the anthers is much narrower than that of *Helonias* and *Ypsilandra*, and more or less rudimentary. Both the inner and the outer filaments of *Heloniopsis* are not adnate basally to an ovary. Whereas, in the two other genera, the inner filaments are adnate basally to an ovary, while the outer filaments are not. Based on all these observations, an attempt was made to trace the evolutionary relationships among the species. The process of the evolutionary change of several characters was also presumed.

When Gray (1859) first established his new genus *Heloniopsis*, he distinguished it from *Helonias*. This means that he regarded *Helonias* as the closest genus to *Heloniopsis*. Similarly, when Franchet (1887) first described his new genus *Ypsilandra*, he compared it with *Heloniopsis*, showing some differences between the two genera. It is apparent that he regarded the two genera as close allies. Krause (1930) classified the three genera, *Helonias*, *Heloniopsis* and *Ypsilandra*, along with some other genera in the same higher taxonomic category (Helonieae of Melanthioideae in the Liliaceae). Kawano and Masuda (1980),

Kawano (1996), and Tanaka (1997a) also regarded the three genera as close allies.

In order to increase clarity regarding the evolutionary relationships among the three genera, and to have a proper taxonomic evaluation of them, it is necessary to conduct detailed comparative studies on various characters.

In this study, several characters of both pistils and stamens were compared in the three genera, and the result is presented here with some remarks on their evolutionary implications.

Materials and Methods

In this study, the following 10 species are dealt with: one species of *Helonias* (*H. bullata* L.), four species of *Ypsilandra* (*Y. yunnanensis* W.W. Smith & J.F. Jeffrey, *Y. alpina* Wang & Tang, *Y. cavaleriei* Lévl. & Vnt., *Y. thibetica* Franch.), and five species of *Heloniopsis* (*H. leucantha* (Koidz.) Honda, *H. umbellata* Baker, *H. kawanoi* (Koidz.) Honda, *H. orientalis* (Thunb.) C. Tanaka, and *H. brevica* Maxim.).

The materials and the research methods employed in this study are the same as those described in my previous papers (Tanaka 1997a, 1997b).

Results and Discussion

In the following description, the name of each species is abbreviated as follows; *Helonias bullata* = **Bu**, *Ypsilandra yunnanensis* = **Y**, *Y. alpina* = **A**, *Y. cavaleriei* = **C**, *Y. thibetica* = **T**, *Heloniopsis leucantha* = **L**, *H. umbellata* = **U**, *H. kawanoi* = **K**, *H. orientalis* = **O**, and *H. brevica* = **Br**.

(1) Pistils

1-A. Styles and stigmata

Helonias (**Bu**) has three separate styles, but their basal parts are often connate to form a very short column (Tanaka 1997a), being up to c. 0.4 mm long. The three separate parts of the styles are c. 1.3–2.4 mm long, strongly recurved outward, and stigmatic on the ventral side. The connation of the three styles is also consistently found in both *Ypsilandra* (Tanaka 1997b) and *Heloniopsis*. In *Ypsilandra*, the proportion of the connate part to the entire length of the styles differs among the species: i.e., in **Y**, styles are triparted (Fig. 1A), with a connate (columnar) part being c. 0.6–1.4 mm long and the three separate parts c. 1.0–1.7 mm long. In **A**, styles are trilobed (Fig. 1B), with a columnar (connate) part being c. 6 mm long and the three lobes c. 0.8–0.9 mm long. In both **Y** and **A**, the ventral side of each lobe is

stigmatic. In **C**, the three styles are entirely connate along their lengths, forming a single columnar structure of c. 1.6–2.6 mm in length, with a depressed capitate stigma at the apex (Fig. 1C). **T** and all the species of *Heloniopsis* have also a columnar style which is formed by the entire connation of the three styles. The columnar style of **T** is c. 5–22 mm long, and the stigma is capitate to depressed capitate in shape (Fig. 1D-a). The style of *Heloniopsis* is c. 2.1–24 mm long, and the stigma is usually a depressed capitate in shape, with an occasional trifflle trilobation (Figs. 1D-b, 1D-c, and 3D).

1-B. Number of ovules

The number of ovules per loculus of an ovary was counted in nine species out of 10. The result is shown as follows, with a range of variation (the lowest number and the highest) except two species **Y** and **C** in which only one count was made respectively, the total number of plants examined (indicated by “pl”), and the total number of loculi examined (indicated by “n”): **Bu**, 8–18 (pl=3, n=22). **Y**, c. 79 (pl=1, n=1). **T**, 56–102 (pl=7, n=8). **C**, c. 55 (pl=1, n=1). **L**, 45–105 (pl=5, n=28). **U**, 59–113 (pl=17, n=44). **K**, 23–78 (pl=5, n=10). **O**, 68–189 (pl=14, n=20). **Br**, 50–175 (pl=36, n=54).

The results of counting in **Bu** and **O** are respectively comparable with the seed numbers of the two species reported by Utech (1978). The relatively low number of the ovules in **K** might reflect its small flower size.

Judging from the above result, **Bu** seems to have a fewer number of ovules than the two other genera.

1-C. Seeds

The seeds of the three genera basically resemble each other (Fig. 2). But there is some difference in the morphology of the seeds between *Helonias* (Fig. 2A) and the two other genera (Figs. 2B, 2C). In *Helonias* (**Bu**), they are flattened fusiform in shape, being c. 4.8–5.2 mm long and 0.8–1.0 mm wide, while in

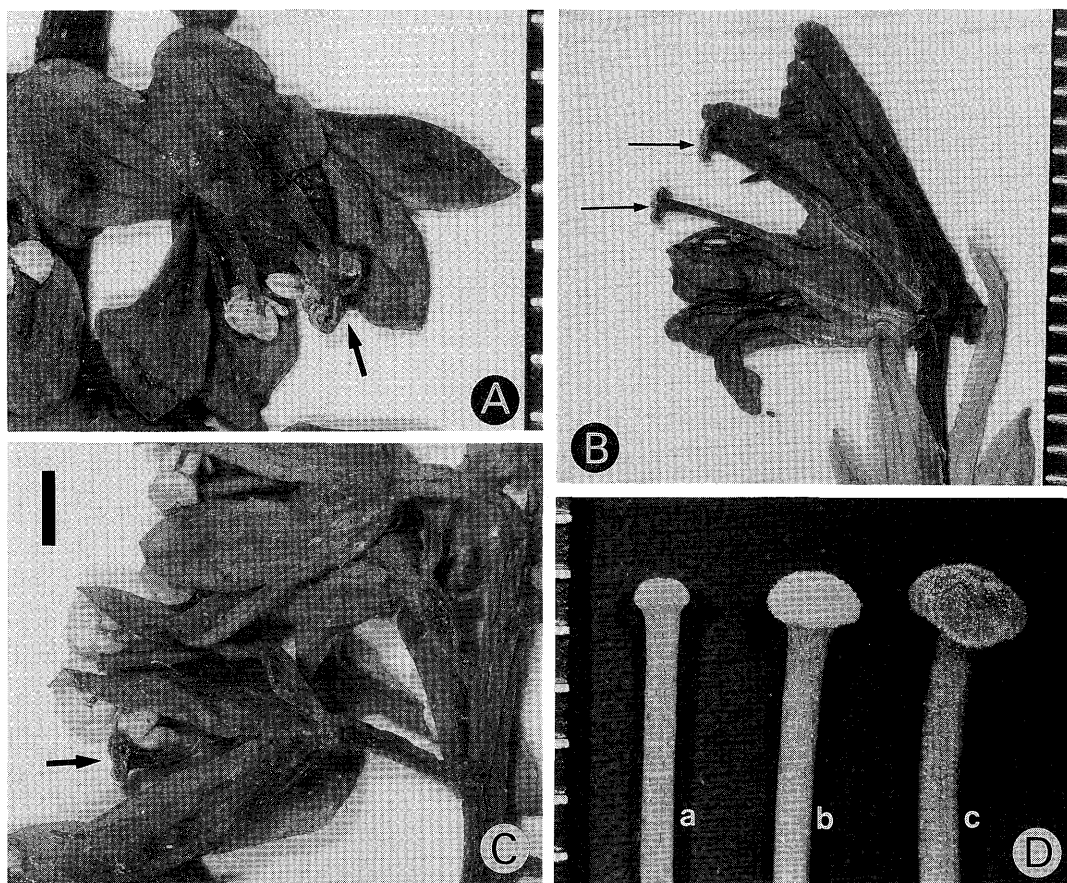


Fig. 1. Styles and stigmata of *Ypsilandra* and *Heloniopsis*. A. *Y. yunnanensis* (G. Forrest, n. 12055, Type, E). B. *Y. alpina* (F. Kingdon Ward, n. 7084, Type, E). Two flowers are overlapped. C. *Y. cavaleriei* (J. Esquirol, n. 2013, E). D. a. *Y. tibetica* (cult. plant in Japan). b. *H. umbellata* (Taiwan, U-1). c. *H. orientalis* (Honshû, O-6). For details of the material see Tanaka 1997a (for *Ypsilandra*) and Tanaka 1997b (for *Heloniopsis*). Arrows in Figs. A–C indicate stigmata. Scales in mm, and the scale bar (Fig. C) equals 1 mm.

the two other genera, they are linear fusiform, being c. 3.3–6.7 mm long and 0.3–0.5 mm wide. The seeds of *Bu* are apparently broader than those of the other two genera.

1-D. Stipe of an ovary

In the two species of *Heloniopsis* (*L* and *U*), it is observed that the stipe is developed at the base of an ovary (Figs. 3A–3C). But there is some intraspecific variation on the development of this stipe in both *L* and *U*; viz., in *L*, the plants from both Isl. Iriomote and Isl. Ishigaki

(Fig. 3A) of the Ryukyu Islands have a distinct stipe, while those from Isl. Okinawa (Hontô: main island) (Fig. 3B, Tanaka 1997b–Fig. 2A) of the same Islands have only a very poorly developed stipe. In *U*, the plants from the same mountain range in northern Taiwan (c.f. Tanaka 1997b, Table 1) also show a similar variation; some have a well-developed stipe (Fig. 3C, Tanaka 1997b–Fig. 2B), while some others do not. In *T*, the basal part of an ovary is observed to elongate slightly after anthesis, forming a

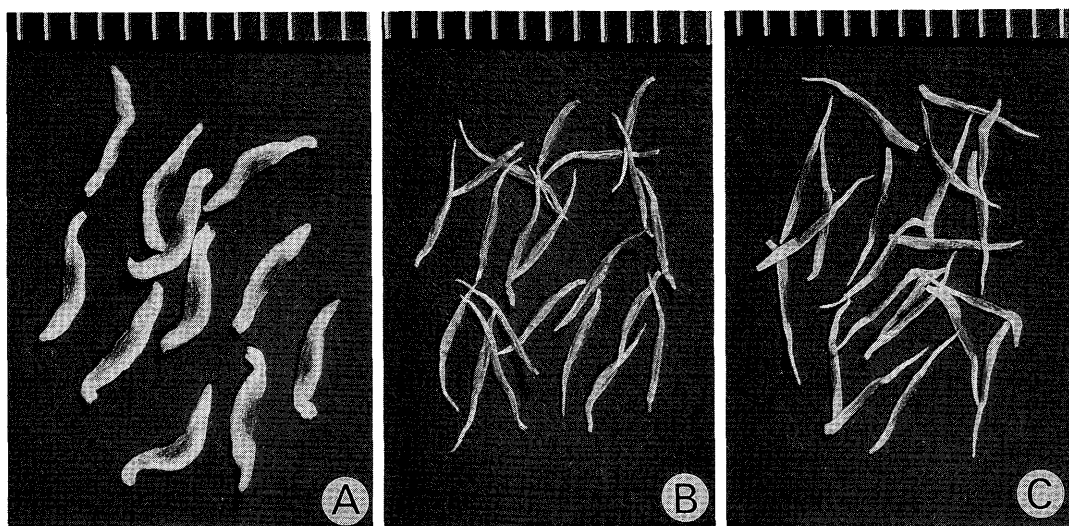


Fig. 2. Seeds of the three genera. A. *Helonias bullata* (New Jersey, K.K. Mackenzie, n. 1209, E). B. *Ypsilandra thibetica* (cult. plant in Japan). C. *Heloniopsis breviscapa* (Kyûshû, B-7). For details of the material see Tanaka 1997a (for *Helonias* and *Ypsilandra*) and Tanaka 1997b (*Heloniopsis*). Scales in mm.

very short stipe (Tanaka 1997a). These facts seem to indicate that *L* and *U* are not only closely related to each other, but also to *T*. Fig. 3D shows a nonstipitate ovary in a flower of *K*. Sessile ovaries of both *O* and *Br* are also seen in Figs. 2C and 2D of Tanaka (1997b).

(2) Stamens

2-A. Anthers

The anthers of *Helonias* are unilocular. There is neither any border nor bordering groove between the upper part of thecae on the dorsal side of the anther, while there is a longitudinal distinct narrow groove between the thecae on the ventral side. But this groove is only externally present and the thecae are practically confluent terminally (Tanaka 1997a). The anthers of *Ypsilandra* are also unilocular, without any such groove on both sides, being shaped like horseshoes (Tanaka 1997a). Both *Helonias* and *Ypsilandra* have a relatively broad confluent part between the neighbouring thecae. On the other hand, it has been reported that the anthers of *Heloniopsis*

are bilocular (Baker 1879, Franchet 1887, Utech 1978, Shimizu 1983). In my observations, the thecae of *Heloniopsis* are also confluent terminally in most cases (Fig. 4), but the confluent part is much narrower than that of both *Helonias* and *Ypsilandra* and more or less degenerative. There is some variation on this confluent part in *Heloniopsis*; e.g., in *L* (Figs. 4A–4C), the confluent part is relatively broad among the species of this genus, while, in some plants of *Br*, the confluent part is very narrow and extremely rudimentary (Fig. 4F).

In *Helonias* and *Ypsilandra*, the confluent part of the anther is relatively broad as stated above, and pollen is produced at both the confluent part and the lateral parts of the anthers. While in *Heloniopsis*, as the confluent part is relatively narrow and in some cases almost rudimentary, it is said that pollen is mostly produced at the lateral parts of the anthers.

The anthers of *Helonias* (Tanaka 1997a) are extrorse, those of *Ypsilandra* are latrorse

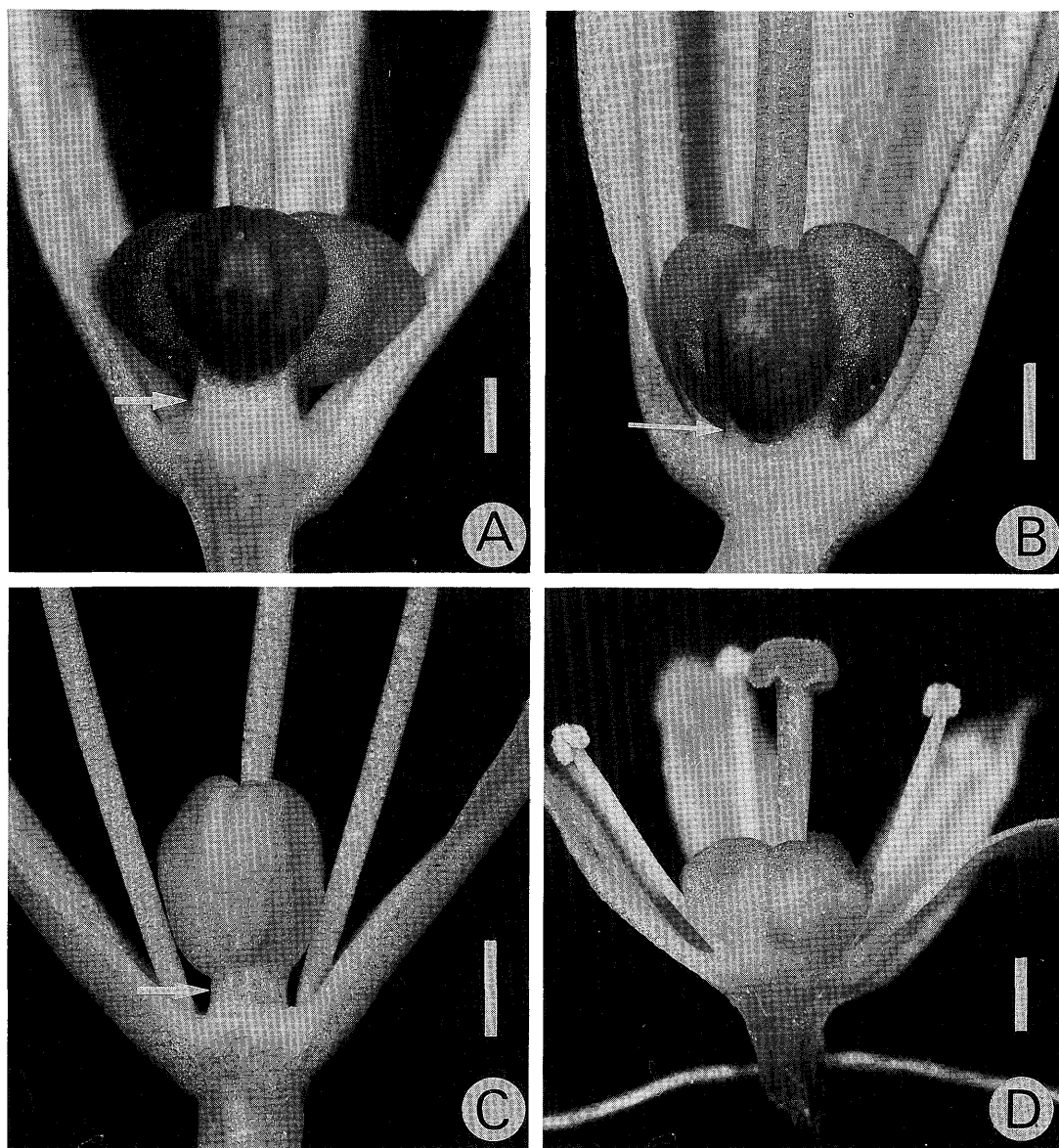


Fig. 3. Basal part of the ovary of *Heloniopsis*. A, B. *H. leucantha* (A: Isl. Ishigaki, L-2. B: Okinawa-hontô, L-1). C. *H. umbellata* (Taiwan, U-2). D. *H. kawanoi* (Isl. Ishigaki, K-1). A and C show stipitate ovaries, B shows an ovary with a poorly developed stipe, and D a nonstipitate ovary. For details of the material see Tanaka 1997b. Bars indicate 1 mm.

(Tanaka 1997a), and those of *Heloniopsis* extrorse to subextrorse (Figs. 4A, 4B, 4D, 4F).

2-B. Filaments

In *Helonias* and *Ypsilandra*, the basal parts of the inner filaments are adnate to the basal

part of an ovary, while the outer filaments are not (Tanaka 1997a). In *Heloniopsis*, both the inner and the outer filaments are not adnate to the basal part of an ovary. Further, in *O* and *Br* the basal parts of both the inner and the outer

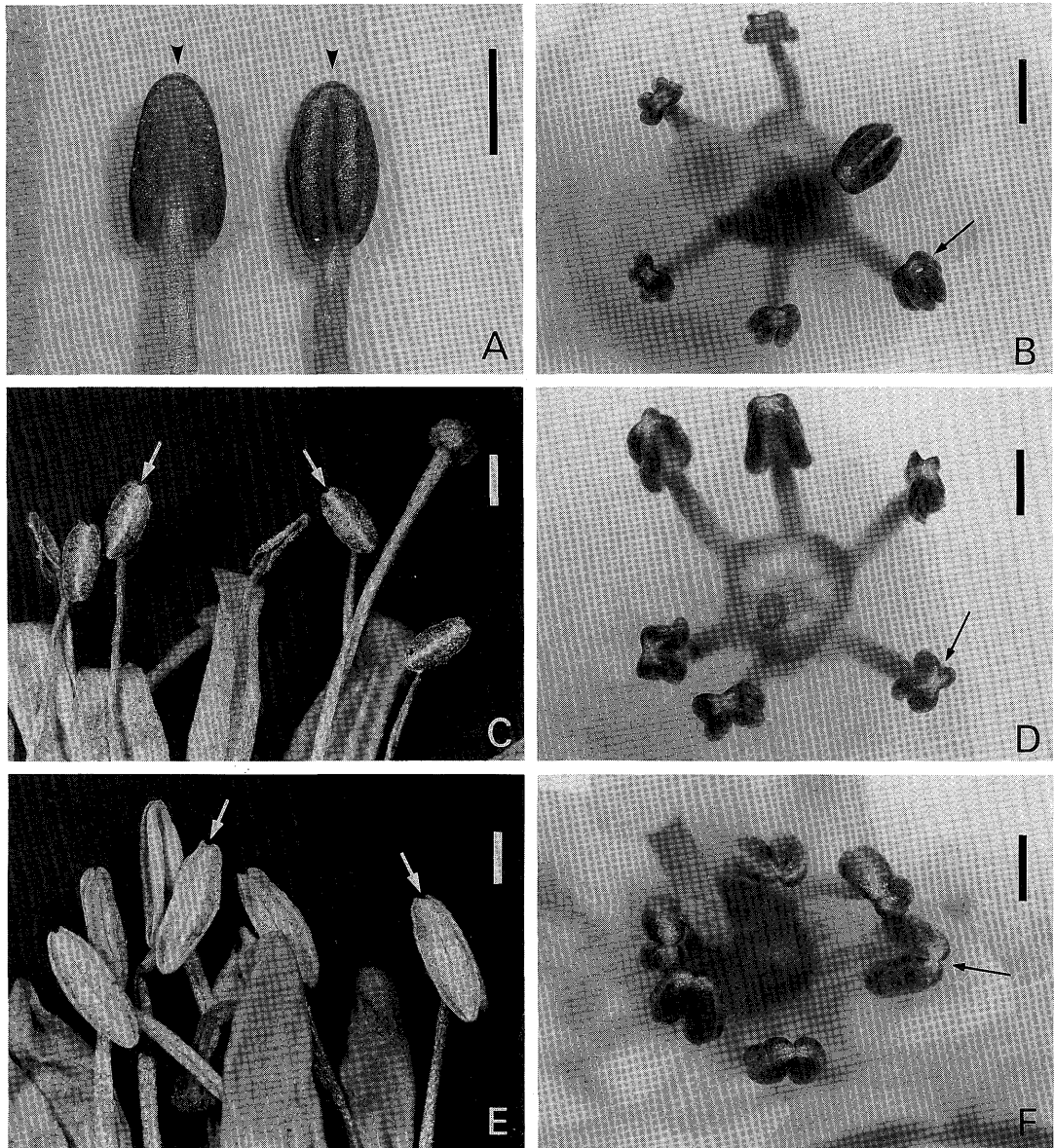


Fig. 4. Anthers of *Heloniopsis*. A–C, *H. leucantha* (Okinawa-hontô, L-1). A. Left; pistil side view. Right; tepal side view. B. Front view of a flower with a focus on the upper part of anthers. C. Dehiscent anthers. D. *H. umbellata* (Taiwan, U-1). The upper part of the style is removed. E. Dehiscent anthers of *H. orientalis* (Honshû, O-8). F. *H. breviscapa* (Kyûshû, B-7). C, E, dried specimens. Note that there is a terminal confluence (indicated by an arrow or an arrowhead) between the thecae. But in Fig. F, it is shown that the confluence between thecae is almost lost (indicated by an arrow). For details of the material see Tanaka 1997b. Bars indicate 1 mm.

filaments are adnate to the basal parts of tepals (Tanaka 1997b).

As a general rule, the structure formed by

the connation of the unitary structures can be regarded as 'secondary' in terms of the organizational level. From this point of view, I pre-

sume that the evolution of the stylar structure of the three genera has proceeded from the three free (or almost free) styles, through intermediate states, to a single columnar style which was formed by the connation of the three styles. If this presumption is correct, the evolution of the species is likely to have proceeded in the following order; $Bu \rightarrow Y \rightarrow A \rightarrow [C, T]$, and the species of *Heloniopsis*. In this scheme, however, the evolutionary relationships among the species within the brackets cannot be clarified only by the stylar character, since all these species have a similar stylar structure. But, if we also take into account some other characters like those described in 1-D, 2-A and 2-B of this report, the following suggestion can be made; viz., *C* and *T* are not only very closely related to each other, but also related to *A* on the one hand, and to *L* and *U* on the other. *C* and *T* seem not to differ qualitatively in any of the characters examined here. Meanwhile, the following suggestions have also been made regarding the evolutionary relationships of the species of *Heloniopsis* (Tanaka 1997b); i.e., *O* and *Br* are more advanced than *L*, *U* and *K* with respect to the floral structure, and *Br* is more advanced than *O* in some floral characters. In the present study, however, the concrete relationships among *L*, *U* and *K* were not clarified. Taking all these observations into account, the evolution of the species of the three genera seems to have proceeded in the following order: $Bu \rightarrow Y \rightarrow A \rightarrow [C, T]^* \rightarrow [L, U, K]^* \rightarrow O \rightarrow Br$ (*the relationships between the species within the brackets require further study).

If this scheme is correct, each of the following characters is likely to have evolved as follows; i.e., the number of ovules per loculus was initially relatively low (*Bu*), but later increased to some extent in *Ypsilandra* and *Heloniopsis* (cf. 1-B). The seeds of *Bu* were

initially relatively broad, but became narrower in and after *Y* (cf. 1-C). Ovaries were at first sessile, but later became stipitate (*T* <in fruit>, *L*, and *U*), and then returned to be sessile (cf. 1-D). Unilocular anthers turned eventually into practically bilocular anthers (cf. 2-A). Anthers were initially extrorse (*Bu*), but later became latrorse (*Ypsilandra*), and then returned to be extrorse to subextrorse (*Heloniopsis*) (cf. 2-A). Inner filaments were initially adnate basally to an ovary (*Helonias* and *Ypsilandra*), but later became free from an ovary (*Heloniopsis*), and then both the inner and the outer filaments became adnate basally to tepals (*O* and *B*) (cf. 2-B).

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田中教之: *Helonias*, *Ypsilandra*, *Heloniopsis* の系統と分類 I. 形質状態の比較(1)

表題の3属(ユリ科)は類似性の高い一群である。これら3属の種の系統的關係と分類の検討を行うため、さまざまな形質について比較研究を行った。本稿では雌ずいと雄ずいのいくつかの形質についての観察結果を報告する。

Helonias の花柱は3ないし3深裂し、*Ypsilandra* の花柱は3中深裂、3浅裂、または細柱状で、花柱が細柱状の場合の柱頭は頭状ないし円盤状である。*Heloniopsis* (ショウジョウバカマ属) の花柱も細柱状で、柱頭は円盤状ないし半球状でしばしばわずかに3裂する。*Helonias* の子房一室当たりの胚珠数は他の2属のそれに比べて少なく、また *Helonias* の種子は他の2属のそれに比べて巾広くややずんぐりしている。子房柄の発達はいずれの2種 (*H. leucantha* と *H. umbellata*) において見られた(ただしそれぞれ種内変異がある)。*Y. thibetica* でも花後に子房基部が少し延長し、柄状となる傾向がある。*Helonias* の葯は前報(Tanaka 1997a)でも記したように一室化しており、この性質は *Ypsilandra* のそれと一致する。ただし、*Helonias* の葯にはその腹面(花被片側)で半葯間に縦溝があるが背面(雌ずい側)にはなく、このような縦溝は *Ypsilandra* にはない。*Heloniopsis* に

おいても、葯の上部は多くの場合、半葯間で連合している。しかし、この連合部分は他の2属のそれと比べてかなり巾狭く、退化的である。この半葯間の連合は *H. leucantha* などでは比較的明瞭であるが、*H. breviscapa* の個体ではほとんど失われている場合がある。*Helonias* と *Ypsilandra* では葯室側部と同様に半葯間の連合部分でも多くの花粉が生産されるのに対して、*Heloniopsis* ではその花粉が主として葯室の側部で生産されることは受粉生物学的観点から興味深く思われる。*Helonias* と *Ypsilandra* の内花糸基部は子房基部と合生するが、外花糸基部は離生する (Tanaka 1997a)。*Heloniopsis* では内外両花糸共にこれらの基部は子房基部と離生する。とくに本属の *H. orientalis* と *H. breviscapa* ではこれらの花糸がさらに花被片基部と合生し鞘状の蜜槽を形成することは既に報告したとおりである (Tanaka 1997b)。本研究で観察された事実と筆者の前報告 (Tanaka 1997a, 1997b) にある事実とを合わせて考察すると、3属の進化は *Helonias* から *Ypsilandra* をへて *Heloniopsis* へと進んできた可能性が極めて高い。

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